四川自贡晚侏罗世西蜀鳄一新种1)

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摘要:记述了四川省自贡市汇东新区自贡市乳品厂发现的西蜀鳄一新种——周氏西蜀鳄(Hsisosuchus chowi sp. nov.)。新种区别于西蜀鳄已知种的特征是:鼻骨后部沿缝合线有一浅的纵凹,额骨的眶缘向上凸起成嵴,沿额骨缝合线也隆起成一微弱的纵嵴,上颞窝的内侧缘向上凸起呈明显的嵴,顶骨具一前中突,侧视颧骨腹缘呈明显的波曲状,眶后骨前侧角约90°,鳞骨后侧突特别拉长,向侧下后方伸展,使鳞骨侧缘明显向内侧弓曲,左右外枕骨的枕髁部分不相接,翼骨的腹中嵴源于翼骨主体部分,内鼻孔位置比较靠前。此外,齿骨外面和夹板骨腹面具有发达的沟和嵴状雕饰,夹板骨参与下颌联合的部分比较长,肩胛片异常扩展,乌喙骨远端宽于近端,肱骨头增厚并强烈向内侧扩展,三角肌嵴发达,桡侧腕骨具发达的尺骨突,尺侧腕骨远端宽于近端,6列荐前部腹部骨板和3列尾部腹部骨板,也可能是周氏西蜀鳄的衍生特征,但这些性状在大山铺西蜀鳄中情况不明,有待更多的材料来证实。

杨钟健、周明镇(1953)在建立西蜀鳄属之初就已注意到西蜀鳄是一种特化的鳄类,认为西蜀鳄不仅将原始特征和进步特征混存于一身,而且还具有一些一般鳄类所没有的独特性质。以此为基础,他们建立了西蜀鳄科。目前西蜀鳄类动物发现并不多,仅有1属2种,即重庆西蜀鳄和大山铺西蜀鳄,而且材料不完整,特别是头后骨骼保存不理想。周氏西蜀鳄的发现不仅扩大了西蜀鳄类的分布范围,而且还增加了我们对这一特化鳄类的认识。

关键词:四川自贡,晚侏罗世,上沙溪庙组,西蜀鳄

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A NEW SPECIES OF HSISOSUCHUS FROM THE LATE JURASSIC OF ZIGONG, SICHUAN, CHINA

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Abstract A crocodyliform specimen collected from the Late Jurassic Shangshaximiao Formation, Zigong, Sichuan Basin, China comprises a nearly complete skull, mandibles, most vertebrae, partial pectoral and pelvic girdles, most forelimbs and osteoderms. It represents a new species of Hsisosuchus, H. chowi sp. nov. Diagnostic features of the new species include a shallow longitudinal depression between nasals; a ridge along orbital margin of frontal; a faint ridge along suture between frontals; a distinct ridge along medial margin of supratemporal fossa; an anteromedian process of parietal wedging between posterior processes of frontals; ventral margin of jugal distinctly waved in lateral view; postorbital having an angular anterolateral corner; posterolateral process of squamosal extraordinarily elongated and extending outwards, downwards and backwards, leading to lateral margin of squamosal distinctly arched medially; exoccipital not contacting its opposite on occipital

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condyle; a ventral median ridge of pterygoid originated from main body of pterygoid; and choana positioned anteriorly. The discovery of *H. chowi* increases not only the distribution but also the understanding of the specialized hisosouchids.

Key words Zigong, Sichuan, Late Jurassic, Shangshaximiao Formation, Hsisosuchus

1 Introduction

Hissosuchus was described by Young and Chow (1953) on the basis of a cranium and some caudal osteoderms of an old individual from the Late Jurassic Shangshaximiao Formation, near Chongqing (Chungking) city. A new family, the Hissosuchidae, was then erected for this genus and species on the basis of a number of peculiar features. To date two species of Hissosuchus have been described. One is the type species Hissosuchus chungkingensis Young et Chow, 1953. The other is Hissosuchus dashanpuensis Gao, 2001 from the Middle Jurassic Xiashaximiao Formation, Dashanpu, Zigong, Sichuan Basin. Li et al. (1994) described a young individual of H. chungkingensis, including the cranium and most of the postcranium, from the Late Jurassic Shangshaximiao Formation, Yongchuan, Chongqing. On the basis of the description, Wu et al. (1994) discussed the phylogenetic relationships of H. chungkingensis.

In 1997, a nearly complete skeleton was collected by workers for the construction of the dormitory of the Zigong Dairy Factory from the red mudstone of the lower part of the Shangshaximiao Formation at Huidong, Zigong, Sichuan, a locality that is 8 km away from the famous dinosaur site of Dashanpu in Zigong, SW China. Here we describe this specimen and erect a new species for it.

2 Systematic paleontology

Crocodylomorpha Walker, 1970
Crocodyliformes Benton et Clark, 1988
Mesoeucrocodylia Whetstone et Whybrow, 1984
Hsisosuchidae Young et Chow, 1953
Hsisosuchus Young et Chow, 1953
Hsisosuchus chowi sp. nov.

(Figs. 1 ~ 4)

Holotype ZDM (Zigong Dinosaur Museum, Zigong) 0146, a nearly complete skull, mandibles, most vertebrae, partial pectoral and pelvic girdles, most forelimbs, fragments of hindlimbs and most osteoderms (Figs. 1 ~ 4).

Horizon and locality Lower part of Shangshaximiao Formation, Huidong, Zigong, southern Sichuan, China; Late Jurassic.

Etymology The specific name is in honor of the late Prof. Chow Minchen, Honorary Director of the Zigong Dinosaur Museum, in memory of his instruction to the senior author.

Diagnosis A medium-sized mesoeucrocodylian distinguishable from the other two known species of *Hsisosuchus* in having a shallow longitudinal depression between nasals; a ridge along orbital margin of frontal; a faint ridge along suture between frontals; a distinct ridge along medial margin of supratemporal fossa; an anteromedian process of parietal wedging between posterior processes of frontals; ventral margin of jugal distinctly waved in lateral view; postorbital having an angular anterolateral corner; posterolateral process of squamosal extraordinarily elongate and extending outwards, downwards and backwards, resulting in lateral margin of squamosal distinctly arched medially; exoccipital not contacting its opposite on occipital condyle; a median ventral ridge of pterygoid originated from main body of pterygoid; and choana positioned anteriorly.

In addition, splenial entering symphysis anteriorly for a relatively long distance, well-sculptured outer surface of dentary and ventral surface of splenial, extraordinarily expanded scapular blade, presence of coracoid foramen, strongly thickened and expanded head of humerus, well-developed deltopectoral crest, a developed process of radiale for ulna, six rows of ventral osteoderms of presacral, and three rows of ventral osteoderms of caudal may be unique to *H. chowi*, but these characters are uncertain in *H. dashanpuensis*.

3 Description

The holotype represents an adult individual with a skull of 12 cm wide (measured across the quadrotojugals) and approximately 25 cm long (measured from the tip of the snout to the level across the posterior margins of the quadrate condyles). Due to a crevice across the skull, some of the cranial bones were damaged. The skull has a narrow anterorbital portion and a suddenly broadened postorbital portion. The snout (the region anterior to the anterior margins of the orbits) is about twice the post-snout region of the skull (from the anterior margins of the orbits to the posterior edge of the cranial table). The cranial table has a slightly convex dorsal surface. The orbits are large and face laterodorsally. The supratemporal fossae are 25 mm long and 21 mm wide, smaller than the orbit. The infratemporal fenestrae are small. Most of the cranial elements are generally well-sculptured with pits, grooves and ridges.

The anterior tips of the premaxillae are slightly damaged. Presumably, the external naris bordered by the nasal and premaxilla is positioned terminally and separated from its fellow by the premaxillae and nasals as in *H. dashanpuensis*. The outer surface of the premaxilla is sculptured except the alveolar portion. Several nutritive openings are present along a line approximately 3 mm away from the alveolar margin. The palatal process of the premaxilla is thin and flat, and contacts its counterpart along the midline of the skull, forming the anterior part of the secondary palate.

The paired maxillae are slightly damaged anteriorly and posteriorly. They are large and have one sinusoidal wave along the alveolar margin, which is as strong as in *H. chungkingensis* but weaker than in *H. dashanpuensis*. A dune-shaped bulge is present in the middle of the maxilla at the level of the fifth maxillary tooth as in *H. dashanpuensis*, rather than at the level of the fourth maxillary tooth as in *H. chungkingensis* and recent *Alligator sinensis* (Cong et al., 1998). The outer surface of the maxilla is sculptured except for the alveolar portion. A row of nutritive openings are present above the alveolar margin. A faint notch close to the nasal at the broken posterior end of the right maxilla probably borders the anterior margin of the antorbital fenestra. The palatal process of the maxilla meets its opposite anteriorly and separates from the latter at the position of the fifth tooth and borders the anterior and lateral edges of the choana. This indicates that the latter is positioned more anteriorly than that in other hisosuchids. The posterior part of the palatal process is narrowed and contacts the palatine medially, ectopterygoid posteriorly and jugal laterally.

The paired nasals are slightly damaged anteriorly and posteriorly. A shallow longitudinal depression is present between the nasals posteriorly (Figs. 1A, 2A). This depression is very deep in *H. chungkingensis* but lacks in *H. dashanpuensis*. The outer surface of the nasal is well-sculptured with dense elongate grooves and ridges, differing from the sculptures of the adjacent bones.

The lacrimals are incomplete. They form the anterior borders of the orbits. The lacrimal foramen is marked on the orbital wall of the bone.

The prefrontals are incomplete. They are narrow, long and triradiate bones and positioned on the anterodorsal corners of the orbits. The descending process is broad and extends ventrolaterally to form the upper anterolateral wall of the orbit.

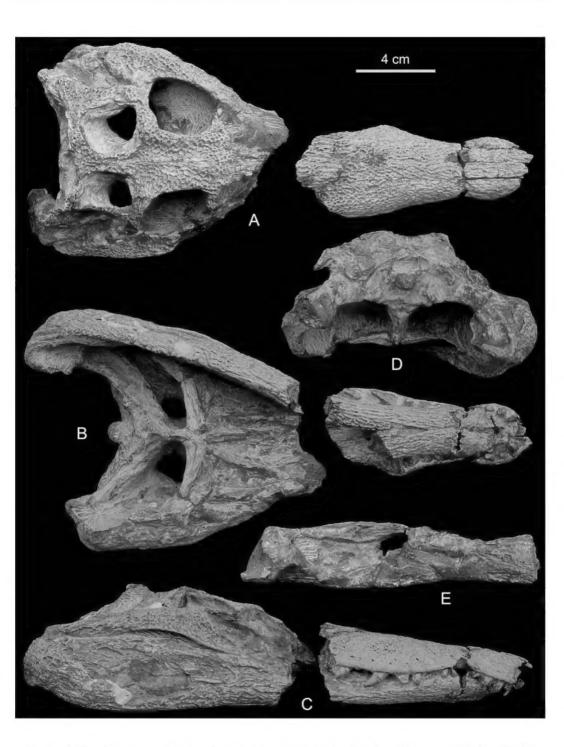


Fig. 1 Skull and lower jaws of *Hsisosuchus chowi* sp. nov. (ZDM 0146) in dorsal(A), ventral (B), right(C) and postrior (D) views, and posterior portion of left lower jaw in medial view (E)

The paired frontals are broad and suturally separated. The interorbital region is 25 mm

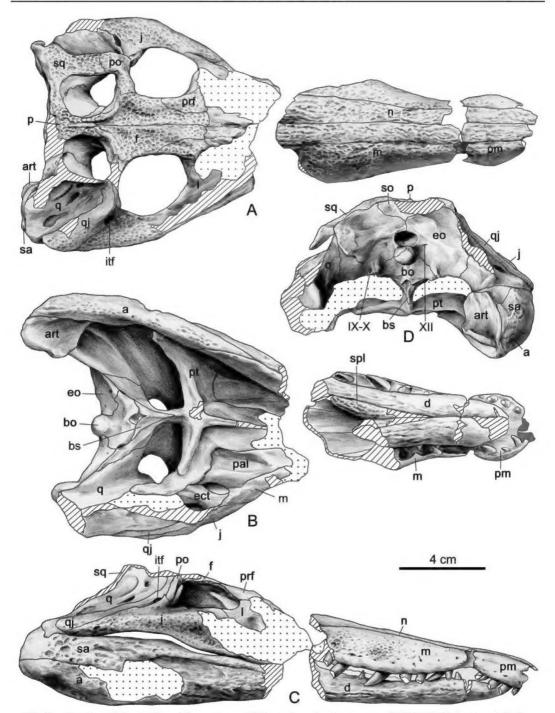


Fig. 2 Drawing of the skull and lower jaws of *Hsisosuchus chowi* sp. nov. (ZDM 0146) in dorsal (A), ventral (B), right (C) and posterior (D) views

Abbreviations; a. angular; art. articular; bo. basioccipital; bs. basisphenoid; d. dentary; ect. ectopterygoid; eo. exoccipital; f. frontal; itf. infratemporal fenestra; j. jugal; l. lachrymal; m. maxilla; n. nasal; p. parietal; pal. palatine; pm. premaxilla; po. postorbital; prf. prefrontal; pt. pterygoid; q. quadrate; qj. quadratojugal; sa. surangular; so. supraoccipital; spl. splenial; sq. squamosal

wide. Differing from that of the other hissosuchids, the orbital margin of the frontal is convex dorsally to form a marginal ridge, and a faint ridge is present along the suture between the frontals. The central portion of the frontal is distinctly concave dorsally. Along the medial margin of the supratemporal fossa, the frontal has a distinct ridge, which extends posteriorly to form a sharp posterior process and overlaps anterolateral margin of the median process of the parietal, unlike the condition in other crocodyliforms.

The unpaired parietal is small. The intertemporal region is very narrow with the smallest width of 7 mm. Anteriorly, the parietal has a median anterior process wedging between the posterior processes of the frontals, unlike the condition in other crocodyliforms. The dorsal surface of the parietal is slightly concave. The anterolateral margins along the supratemporal fossae are slightly convex to form ridges. The posteromedian process is uncertain, while as in *H. chungkingensis*, the parietal does not expand posteriorly to overhang the occiput. Within the supratemporal fenestra, the parietal floors the medial portion and enters into the medial border of the foramen for the temporo-orbital artery.

The paired jugals have a broad anterior process and a narrow posterior process. The ventral margin of the jugal is distinctly waved in lateral view (Figs. 1C, 2C), unlike the condition of other hisosuchids. As in *H. chungkingensis*, the well-sculptured outer surface of the jugal is curved at about 90° along the midline of the bone. The ascending process of the jugal is short and flat. It contacts the anterodorsal process of the quadratojugal dorsally, separating the postorbital from the infratemporal fenestra. The posterior process contacts the quadratojugal at a straight oblique line.

The postorbitals are small, with a typical angular anterolateral corner so that the skull table is typical crocodyliform-like. In *H. chungkingensis*, the anterolateral corner of the postorbital is about 145°. Its descending process extends along the anterior side of the postorbital bar to the ventral edge of the orbit and separates the ascending process of the jugal from the orbit. The unsculptured postorbital bar is slightly sunken beneath the bone surface.

The paired squamosals are triradiate and form the posterolateral portions of the skull table. Laterally, the squamosal is thickened and suspends above the external otic recess and bears a groove for the attachment of the ear flap. The posterolateral process of the squamosal is extraordinarily elongated and extends outwards, downwards and backwards. As a result, the lateral margin of the squamosal is distinctly arched medially, rather than slightly arched laterally as in *H. chungkingensis*. Medially, the squamosal makes contribution to the floor of the supratemporal fossa. On the occipital surface, it contacts the supraoccipital and encloses the external otic recess from the back.

The quadratojugal is thin and broad, and extends obliquely. Its anterodorsal process contacts not only the squamosal and postorbital, but also the ascending process of the jugal. The posteroventral end is slightly thickened, but does not appear to be part of the jaw articular condyle. The ventral portion close to the jugal is well sculptured, but the remaining portion is unsculptured. The small infratemporal fenestra is bordered by the quadratojugal and jugal.

The quadrate is a large, but hollow bone extending backwards, downwards and outwards along the side of the braincase. It has a distinct distal portion and a gently curved posterior edge. Its dorsal surface is heavily fenestrated. The lateral mandibular condyle is stronger than the medial one. The line between the posterior end of the quadrates is not only much lower than the occipital condyle in vertical plane, but also much more posterior than the latter in horizontal plane. The anterodorsal process of the quadrate extends into the supratemporal fenestra and then turns upwards to form the posterolateral wall of the supratemporal fenestra. The pterygoid process expands laterally to the quadrate process of the pterygoid.

The occipital surface is concave anteriorly and has a strong transverse ridge extending along a level dorsal to the foramen magnum (Figs. 1D, 2D). The foramen magnum is oval-shaped

with 12 mm wide and 9 mm high. The occipital condyle is rounded with short but stout neck. The supraoccipital is a triangular bone. It is excluded from the foramen magnum because of the contact between the exoccipitals dorsal to the foramen magnum. The dorsal margin of the supraoccipital does not contribute to the cranial table, unlike the condition in late crocodyliforms.

The exoccipital is large and occupies most of the occipital surface. It is divided into large upper and small lower portions by a transverse ridge as in most crocodyliforms. The paroccipital process of the exoccipital extends laterally to a lesser degree than the squamosal. A groove is present between this process and the quadrate. The medioventral portion of the exoccipital is convex posteriorly and forms a small part of the occipital condyle medially, but does not contact its opposite ventral to the foramen magnum as in *H. dashanpuensis*. In *H. chungkingensis*, the occipital condyle is entirely formed by the basioccipital. An opening, close to the foramen magnum, probably serves for the exit of cranial nerve XII. Another ventrally positioned opening probably serves for the cranial nerves IX-X and the carotid artery.

The basioccipital forms most of the occipital condyle. Its ventral portion is butterfly-shaped and oblique in orientation. It has a concave posteroventral surface and strongly thickened lateral margins. The anterior end of the basioccipital is W-shaped. Three foramina for the eustachian tube are located at the boundary between the basioccipital and basisphenoid.

The basisphenoid is small and triangular in outline. It inclines anteroventrally and forms a faint crotched ridge. The anterior end of the basisphenoid lacks basipterygoid process.

The pterygoid is well-developed. Its main body has a stout transverse ridge, resulting in a deep step between this body and the palatal process. The palatal process is thin and plate-like, and extends anteriorly with a concave ventral surface. The lateral margin of the palatal process contacts the palatine, forming a laterally arched ridge as in other hisosuchids. As in *H. dashanpuensis* and the adult specimen of *H. chungkingensis*, a median ridge is present, but this ridge originates from the main body of the pterygoid (Figs. 1B, 2B), rather than from the palatal process of the pterygoid as in *H. dashanpuensis* and the adult specimen of *H. chungkingensis*. In the juvenile specimen of *H. chungkingensis*, the pterygoid lacks the median ridge. The choanae are uncertain because the anterior portions of the pterygoid and palatine are damaged. They are probably positioned anteriorly as in *H. dashanpuensis*. The quadrate process of the pterygoid extends posterolaterally and contacts the basioccipital and pterygoid process of the quadrate.

The ectopterygoid is small, relative to that of *H. dashanpuensis*. It is compressed and twisted, with slightly expanded anterolateral and posteromedial ends. It extends forwards, outwards and upwards from the lateral margin of the pterygoid, and contacts the jugal to form the pillar between the primary and secondary palatal arches. As in *H. dashanpuensis*, the suborbital fenestra is small and split-like, while it is closed in *H. chungkingensis*.

The palatines are damaged anteriorly. They are thin and long, with distinctly concave ventral surfaces. The anterolateral margin contacts the palatal process of the maxilla. The posterolateral margin forms the medial edge of the suborbital fenestra. The medial margin contacts the palatal process of the pterygoid and forms a laterally arched ridge.

The symphysis of the lower jaws is long with a length of 6.5 cm. Posterior to the symphysis, the mandibular rami diverge at a small angle and then turn medially posterior to the external fenestra. The external mandibular fenestra is small and oval-shaped (Figs. 1C, 1E). The dentary is long and compressed. It is well-sculptured with longitudinal grooves and ridges except for the alveolar portion. In the type of *H. chungkingensis*, it is slightly sculptured with few longitudinal grooves and ridges, and in the junvenile specimen of *H. chungkingensis* it is unsculptured. The lateral surface of the dentary is distinctly curved along a line between the lower sculptured portion and the unsculptured alveolar portion, forming a longitudinal groove

and a ridge.

The splenial is long and deep and enters the symphysis anteriorly for a relatively long distance. Its posterior end reaches the mandibular fossa. The ventral margin of the splenial is thickened in the middle portion and contacts the dentary at a straight line. In ventral view, the splenial is willow leaf-like, and the ventral surface is well sculptured (Figs. 1B, 2B), unlike the condition in *H. chungkingensis*.

The angular is a long, deep and trough-like bone and serves as the medial wall of the adductor chamber. Anteriorly, the angular tapers to a point and is wedged between the dentary and splenial, and posteriorly it extends to the ventral side of the retroarticular process. The outer surface of the angular is well sculptured.

The surangular is long and arched dorsally, forming the posterodorsal portion of the mandibular ramus. Its anterior portion is shallow and attaches to the dorsal margin of the posterior portion of the dentary and splenial. Its posterior portion is deep and covers the lateral surface of the articular. The lateral surface of the surangular is sculptured with pits and ridges.

The articular, mostly covered laterally, posteriorly, and ventrally by the angular and surangular, is robust and short, and forms the broad, dorsally positioned articular fossae. The retroarticular process of the articular is moderately developed and slightly-dorsally positioned.

Four right and three left premaxillary teeth are preserved. According to the condition of the premaxilla, the premaxillary dentition presumably consists of five teeth on each side as in *H. dashanpuensis*. Of them, the fourth tooth is the largest. The premaxillary teeth are conical and slightly recurved, lacking ridges or serrations on the anterior and posterior edges except for the posterior edge of the posteriormost two premaxillary teeth with a faint ridge.

Eight right and two left incomplete maxillary teeth are preserved. The complete maxillary dentition is uncertain, but the condition of the right maxilla infers that the maxillary dentition has more than ten teeth on each side. The maxillary tooth is slightly compressed and recurved, with serrations on the anterior and posterior edges. The fifth tooth is the largest among the maxillary dentition as in *H. dashanpuensis*.

The dentary dentition is uncertain because of the occlusion of the upper and lower jaws. The morphology and structure of the dentary tooth are similar to that of the maxillary tooth.

Five cervicals, 3rd, 4th, 6th, 7th and 9th, are preserved in some degree. The cervicals 3rd and 4th (Fig. 3A) are coeloplatyan and have a weak hypapophysis and a well developed median ridge on the ventral surfaces. Their neural spines are high and their prezygapophyses are well developed. An oblique ridge is visible on the lateral surface of the neural spine. The centrum of the cervical 6th is short and has a well-developed hypapophysis and median ridge. The parapophyses are closed to the transverse process. Both the prezygapophysis and postzygapophysis are well developed (Fig. 3B). The neural spine is narrow but high, with slightly expanded dorsal end and thin anterior and posterior edges. The cervical 7th lacks its centrum and neural arch. The cervical 9th is articulated with the dorsal vertebrae.

Fifteen amphicoelous dorsal vertebrae are preserved in articulation except for the last one (Figs. 3C, 3D). Most of them are enclosed by osteoderms. The centra of the first two dorsals are small and short, and have a hypapophysis. The centra of the dorsal 3rd ~ 5th lack hypapophysis but have a faint median ridge. The centra of the remaining posterior dorsals are short but robust and lack hypapophysis and median ridge in ventral surface. All of the dorsals have well developed transverse processes and a broad, plate-like neural spine with an expanded dorsal end. The neurocentral suture is visible in the posterior dorsals.

Two articulated amphicoelous sacrals are completely preserved with the sacral ribs (Figs. 3E ~ G). The centra are the largest ones among the vertebral column and oval-shaped in anterior or posterior view. The ventral surface of the first sacral bears a deep groove posteriorly. This groove extends to the anterior portion of the second sacral. The neural arch of the first

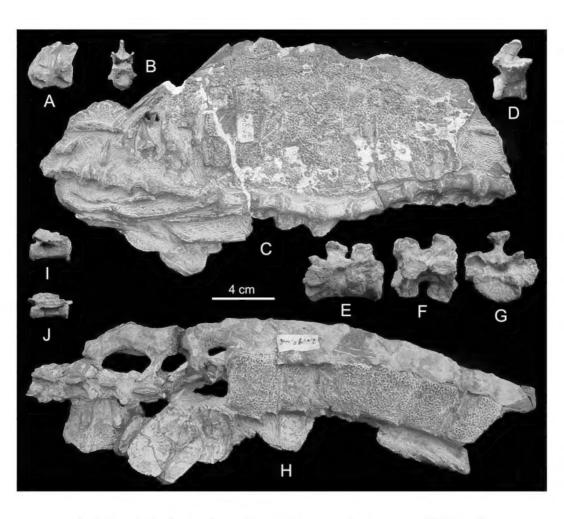


Fig. 3 Vertebral column and osteoderms of *Hsisosuchus chowi* sp. nov. (ZDM 0146)

A. left view of cervicals 3rd and 4th; B. anterior view of cervical 6th; C. ventral view of posterior presacrals and ventral osteoderms; D. right view of dorsal 15th; E. left view of sacrals; F. dorsal view of sacrals; G. anterior view of sacral 1st; H. dorsal view of anterior caudals and dorsal osteoderms; I. right view of a middle caudal; J. right view of a posterior caudal

sacral is lower than that of the second. The neural spine of the first sacral is shorter than that of the second. The dorsal end of the neural spines of the sacrals are expanded laterally to form a platform, but this platform in the first sacral is more distinctive than in the second one. Both the prezygapophyses and postzygapophyses of the sacrals are well developed. The ribs of the sacrals are fused with the transverse process, forming a thickened plate. The distal end of the sacral rib is strongly expanded and forms a broad articulated surface with the ilium.

Fifteen amphicoelous caudal vertebrae are preserved (Figs. 3H ~ J). Of them, 12 articulated caudals belong to the anterior region. The other three unarticulated caudals belong to the middle and posterior regions respectively. The first caudal is robust and short. The remaining anterior caudals progressively become slender and longer. By the caudal 12th, the length of the centrum is more than twice the width. The ventral surfaces of the first two caudals are rounded with no ridge and groove. A shallow groove appears in the posterior portion of the

ventral surface of the caudal 3rd, and this groove progressively extends anteriorly and becomes more distinctive in the remaining anterior caudals. The transverse process of the anterior caudals is long and extends laterally, but becomes progressively shorter posteiorly. In the posterior caudals, the transverse process becomes a longitudinal ridge. The neural spine of the anterior caudals is short but high. It becomes progressively longer and lower posteriorly. The dorsal end of the neural spine is slightly expanded.

The complete left scapula and the distal portion of the right scapula are preserved. The scapular blade is proportionately higher and broader than that of *H. chungkingensis* because the proximal portion is strongly expanded anteroposteriorly (Fig. 4A). The dorsal margin is slightly arched, with a length of 6 cm. The anterodorsal margin is thin and strongly arched, and much shorter than the slightly curved and thickened posteroventral one. The portion below the neck is expanded and curved medially. The distal end is distinctly thickened, forming the upper half of the glenoid surface. The acromial ridge is well developed and extends along the anterior margin of the ventral portion of the scapula. The articular facet for the coracoid is ear-like, with a narrow anterior portion and a broad posterior portion. The glenoid process at the posteroventral corner is thickened. A distinct depression between the acromial ridge and glenoid process is present on the lateral surface of the scapula.

The coracoid is half as long as the scapula. The coracoid foramen is present in the middle of the dorsal portion, unlike the condition in *H. chungkingensis*. The dorsal portion is expanded anteroposteriorly to match the lower end of the scapula, while the posterior margin is thickened to form the lower half of the glenoid. The shaft of the coracoid is compressed and slightly distorted. The distal end is extraordinarily expanded anteroposteriorly, being broader than the dorsal end, and forms the foot-like processes anteriorly and posteriorly (Fig. 4B).

The left humerus and the proximal half of the right humerus are preserved. In comparison with *H. chungkingensis*, the head is more strongly expanded and thickened, with a lip-shaped articular surface, the deltopectoral crest is more pronounced, the shaft is straight and stronger, and the distal portion is distinctly expanded (Fig. 4C).

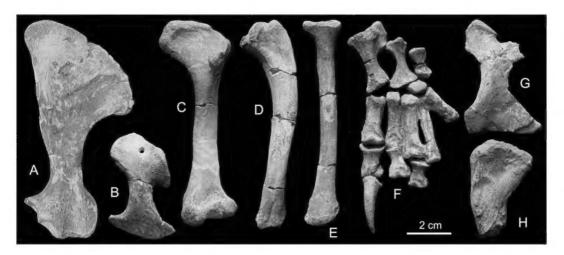


Fig. 4 Elements of pectoral and pelvic girdles of Hsisosuchus chowi sp. nov. (ZDM 0146)
A. medial view of left scapula; B. lateral view of left coracoid; C. anterior view of left humerus; D. posterior view of right ulna; E. medial view of right radius; F. dorsal view of left manus; G. lateral view of right fibula

The complete right ulna has an extraordinarily expanded proximal end. The coronoid process is developed but slightly ventrally positioned. The olecranon process is somewhat pronounced but less well developed. The shaft is slightly compressed and distinctly arched laterally (Fig. 4D). The distal end is less expanded, with a slightly convex surface for the radiale and a developed styloid process bent upwards.

The right radius is complete (Fig. 4E) and the left radius is represented by the distal portion. It is shorter than the ulna. The proximal and distal ends are expanded. The shaft is straight and slender, and slightly twisted.

Of the elements of the manus, the radiale is the largest and longest. It is compressed, with the slender shaft and the distinctly expanded proximal and distal ends. As in most crocodyliforms, the proximal end extends to the ulna to form the process for the ulna (Fig. 4F). This process lacks in *H. chungkingensis* (Li et al., 1994, fig. 6).

The ulnare is much smaller and shorter than the radiale. Both the proximal and distal ends are distinctly expanded, while the distal end is broader than the proximal end.

The pisiforme is compressed and much shorter than the ulnare. The proximal and distal ends are slightly expanded. The proximal surface articulates the styloid process of the ulna.

One distal carpal is preserved in each manus. Presumably only one distal carpal is ossified. The distal carpal is thick and anteroposteriorly shuttle-shaped. The dorsal surface is distinctly convex and has two facets for the ulnare and pisiforme respectively. The ventral surface is concave and saddle-shaped, in articulation with metacarpals III, IV and V.

All the five metacarpals are long and slender, with the expanded proximal and distal ends and straight, cylinder-shaped shaft. The dorsal surface of each metacarpal is flat and the ventral surface is concave. Distally, there is a distinct pit on the dorsal surface for preventing the digit from reverse. The distal end is distinctly expanded and forms a trochlea-shaped articular surface. Of the metacarpals, metacarpal I is the strongest, metacarpal IV is the longest, and metacapal V is the shortest.

The phalanges are similar to the metacarpals in shape except for the claws, while they are much shorter than the metacarpals. Of the phalanges, the elements of the digit I are the longest and strongest. The claw of digit I is long, compressed and arched dorsally, with an expanded proximal end and sharp distal end. A longitudinal groove is separately present on the medial and lateral surfaces.

The pelvic girdle is represented by the right ischium (Fig. 4G). It is compressed and broadened. The proximal portion is expanded to form the iliac process and pubic process, and borders the acetabulum posteroventrally. The shaft is strongly arched laterally, with thin anterior margin and thick posterior margin. The distal portion is thinner and extraordinarily expanded anteroposteriorly, forming the sharp and foot-like anterior and posterior processes.

The hindlimbs are represented by the distal shaft of the left tibia and the proximal portion of the right fibula. The shaft of the tibia is strong and oval to triangular in shape in cross section. The proximal portion of the fibula is compressed and expanded posterolaterally, forming the triangular-shaped head (Fig. 4H). The tuberculum of the fibula is well developed.

Most of the dorsal and ventral osteoderms of the presacral and caudal are preserved (Figs. 3C, 3H). They resemble those of primitive crocodyliforms such as *Protosuchus* (Colbert and Mook, 1951), *Sunosuchus* (Wu et al., 1996) and *Sichuanosuchus* (Peng, 1995, 1996) except for the absence of an anterolateral process of the dorsal ones. As in most crocodyliforms, the dorsal osteoderms are arranged in two rows. The large and thick dorsal osteoderms of the presacral are rectangular-shaped, and their lateral portion curves ventrally to form a longitudinal ridge. The outer surface is well sculptured with pits and ridges except for the anterior margin covered by the anterior osteoderm. The ventral osteoderms of the presacral are smaller than the dorsal ones, and lack the smooth anterior margin. They are arranged in six rows, rather than in

five rows as in *H. chungkingensis*. The osteoderms of the caudal are smaller than those of the presacral. The ventral osteoderms of the caudal are arranged in three rows, rather than in four rows as in *H. chungkingensis*.

4 Discussion

Histosuchus chowi is the best represented within Histosuchus and the third species of the genus. H. chungkingensis, H. dashanpuensis and H. chowi are considered congeneric on the basis of the following unique characters: 1) presence of antorbital fenestra; 2) ascending process of jugal excluded from orbit by descending process of postorbital; 3) presence of a strong transverse ridge on ventral surface of pterygoid, resulting in a deep step-like structure between palatal process and main body of bone; 4) exoccipital forming a pronounced transverse ridge above foramen magnum; 5) descending process of postorbital excluded from infratemporal fenestra by anterodorsal process of quadratojugal and ascending process of jugal; 6) snout about twice as long as postorbital region; 7) orbit large while supratemporal fenestra small; 8) interorbital region broad while intertemporal region narrow; 9) infratemporal fenestra small; 10) maxillary and dentary teeth compressed with serrations on anterior and posterior edges; and 11) unsculptured postorbital bar slightly sunken beneath bone surface.

However, *H. chowi* can be distinguished from the other two species of *Hsisosuchus* by the following apomorphic characters: 1) longitudinal depression between nasals faint; 2) presence of a ridge along orbital margin of frontal and a faint ridge along suture between frontals; 3) presence of a distinct ridge along the medial margin of supratemporal fenestra; 4) parietal having a median anterior process; 5) ventral margin of jugal distinctly waved in lateral view; 6) postorbital having an angular anterolateral corner, rather than a primitive rounded one; 7) posterolateral process of squamosal extraordinarily elongated and extends outwards, downwards and backwards so that lateral margin of squamosal arched medially; 8) exoccipital not in contact with its opposite on occipital condyle; and 9) choana positioned anteriorly.

In addition, in *H. chowi* the outer surface of the dentary and the ventral surface of the splenial are well-sculptured with elongate grooves and ridges except for alveolar portion of dentary, the scapular blade is extraordinarily expanded, the coracoid foramen is present, the distal end of the coracoid is broader than the proximal end, the head of the humerus is strongly thickened and expanded medially, the deltopectoral crest is well-developed, the radiale has a well-developed process for the ulna, the distal end of the ulnare is broader than the proximal end, and the ventral osteoderms of the presacral are arranged in six rows and those of the caudal are arranged in three rows. These features differ from those of *H. chungkingensis* and may be unique to *H. chowi*, but these characters are uncertain in *H. dashanpuensis*.

Apart from the aforementioned features, H. chowi also differs from H. chungkingensis in the maxilla that have a dune-shaped bulge at level of fifth maxillary tooth, the outer surface of the nasal is well-sculptured with dense elongated grooves and ridges, the suborbital fenestra is present, and fifth maxillary tooth is the largest among maxillary dentition. H. chowi differs from H. dashanpuensis in having a shallow posteromedian depression between the two nasals and the jugal curved at about 90° along midline.

Hsisosuchus was recognized as a specialized crocodyliform when it was erected by Young and Chow (1953). It possesses not only many primitive and derived features but also some unique characters, and consequently the Hsisosuchidae was erected. Li et al. (1994) summarized nine autapomorphic characters of the species. H. dashanpuensis described by Gao (2001) shows that three characters, an elongate posteromedian depression between nasals, suborbital fenestra enclosed and elliptical choana elongated and surrounded by a distinct ridge, are not synapomorphic characters of the genus. The new specimen described in this paper

indicates that the absence of the coracoid foramen is a derived character of the species *H. chungkingensis*, rather than that of the genus. As a result, the diagnoses of the genus *Hsisosuchus* can be revised as: presence of antorbital fenestra, ascending process of jugal excluded from orbit by descending process of the postorbital, presence of a strong transverse ridge on ventral surface of pterygoid, resulting in a deep step-like structure between palatal process and main body of bone, and exoccipital forming a pronounced transverse ridge dorsal to foramen magnum.

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